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Diet and Bioenergetics of Lake-Rearing Juvenile Chinook Salmon in Lake Washington

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Abstract.—Use of lake habitats by ocean-type Chinook salmon *Oncorhynchus tshawytscha* is rare under natural conditions. We studied aspects of the trophic ecology of naturally and hatchery-produced juvenile Chinook salmon rearing in the littoral zone of highly urbanized Lake Washington in Washington State. During February through May, naturally produced juvenile Chinook salmon occupied littoral habitats and consumed mostly epibenthic prey, primarily chironomid pupae (Diptera). In June, they switched to a diet dominated by plankton, specifically *Daphnia* spp. This diet shift from littoral prey to limnetic prey coincided with increasing temperature, a shift by the fish from littoral to limnetic habitats, the spring bloom of *Daphnia*, and increasing fish size. Bioenergetics modeling for these populations estimated that naturally produced juvenile Chinook salmon had high consumption rates and were generally feeding close to their maximum ration, even after large numbers of hatchery-produced Chinook salmon entered the lake. The feeding rates, growth rates, and proportions of maximum daily ration from the modeling suggested that under current conditions, both naturally produced and hatchery-produced juvenile Chinook salmon were finding ample food in littoral habitats of Lake Washington. These results further reveal that hatchery-produced Chinook salmon did not compete with naturally produced fish and that this was probably a result of hatchery juveniles entering the lake during the spring *Daphnia* bloom when this prey is abundant. Our results suggest that managers should focus Chinook salmon recovery efforts in the Lake Washington basin on other aspects of the species' lake use, such as predation or disease, or on other life stages (e.g., spawning adults).

Populations of Chinook salmon *Oncorhynchus tshawytscha* occur as stream and ocean types based on juvenile out-migration characteristics (Carl and Healey 1984; Healey 1991; Teel et al. 2000; Rasmussen et al. 2003). Stream-type Chinook salmon populations generally migrate to sea after rearing for

at least a year in freshwater. Ocean-type populations migrate to sea early in their first year of life, spending only a short period rearing in freshwater, but reside for longer periods in estuarine and nearshore habitats.

Rearing in lakes is rare for ocean-type Chinook salmon populations under natural conditions (e.g., Burger et al. 1985). Recently, some ocean-type Chinook salmon populations have had to incorporate lacustrine habitats into their life histories due to anthropogenic modifications such as the conversion of free-flowing portions of rivers into reservoirs for hydropower (e.g., the Columbia River basin). Where

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lake use by juvenile ocean-type Chinook salmon does occur, anthropogenic disturbances such as overwater structures, shoreline revetments, altered hydrological regimes, introductions of exotic species, and degraded water quality are also often present. Little is known about use of lacustrine habitats by juvenile ocean-type Chinook salmon (Tabor et al. 2004; Sergeant and Beauchamp 2006), and much of this information comes from studies of Columbia River reservoirs (e.g., Dauble et al. 1989; Rondorf et al. 1990; Curet 1993; Tabor et al. 1993; Garland et al. 2002). To better manage existing populations and aid in designing recovery strategies for ocean-type Chinook salmon using lacustrine environments, basic information on the ecology of juvenile Chinook salmon rearing in this habitat is needed.

We identified prey resources and evaluated the bioenergetics of naturally produced juvenile Chinook salmon in Lake Washington, Washington, to examine rearing in a unique, highly modified setting where large numbers of hatchery fish also occur. The Lake Washington basin supports naturally spawning populations of lake-rearing Chinook salmon that were listed in 1999 as threatened by the U.S. Government under the Endangered Species Act (U.S. Office of the Federal Register 1999). Juvenile and adult Chinook salmon must use Lake Washington to migrate to and from spawning areas. Prior to 1917, the Lake Washington basin was part of the greater Green–Duwamish River watershed (Figure 1). As part of the hydrologic modification of the system at that time, the Cedar River, which previously joined the Black River below the outlet of Lake Washington, was redirected into the lake and a new outlet was constructed through the Lake Washington Ship Canal and the Hiram Chittenden Locks (Ajwani 1956; Chrzastowski 1983). While historic use of the watershed by these salmon is not known, it is possible that they did not use the lake until after 1917, when the lake's outlet was changed to the Lake Washington Ship Canal.

The objectives of our study were to (1) determine variability in the diet of juvenile Chinook salmon in littoral areas of Lake Washington with respect to time of year and fish size, (2) evaluate whether diets differed between hatchery and wild juvenile Chinook salmon when they co-occurred in the lake, (3) evaluate fish consumption rates using bioenergetics simulations, and (4) evaluate the implications of our results within the context of food limitations and recovery of these populations. We focused on littoral areas of Lake Washington because shallow aquatic habitats are heavily used by juvenile Chinook salmon in freshwater rearing areas (Dauble et al. 1980; Levings et al. 1991; Tabor et al. 1993, 2004; Garland et al. 2002; Tiffan et al. 2002; Sergeant 2004). In addition, the Lake Washington shoreline has been substantially altered by anthropogenic development (Toft 2001) and Chinook salmon populations using the lake may be affected by these alterations. For example, shoreline development may affect the growth of juvenile Chinook salmon by altering the types and availability of invertebrate prey (White 1975; Northcote and Northcote 1996). The release of large numbers of hatchery Chinook salmon into the lake may represent an additional threat to naturally produced Chinook salmon if wild fish lack sufficient food resources.

Study Area

The Lake Washington basin is located in the Central Puget Sound region of Washington State. Human population in the basin exceeds 1 million, and residential, commercial, and industrial land uses dominate (Fresh and Lucchetti 2000). The basin encompasses about 1,600 km^2, and elevations range from sea level to approximately 1,600 m. Lake Washington is the fourth largest lake in Washington; it has a surface area of 8,959 ha, a mean width of 2.4 km, a length of 32.2 km, a maximum depth of 65 m, and approximately 128 km of shoreline. The Cedar River is the lake's largest tributary, accounting for about half of the mean annual surface flow into the lake (King County 1993). The Lake Washington basin drains to Puget Sound through the Lake Washington Ship Canal, a heavily developed, artificial waterway 13.8 km long. Anadromous fish enter and leave the system at the west end of the Ship Canal at the Hiram Chittenden Locks (Figure 1).

Most Chinook salmon spawning occurs in Issaquah Creek, Big Bear Creek, and the Cedar River (Figure 1). Trapping of downstream-migrating Chinook salmon on the Cedar River and Big Bear Creek indicates that juveniles enter the lake from at least mid-January through late June (Seiler et al. 2004); two distinct groups of fish enter Lake Washington from each tributary (Figure 2). The first group ("early fish" < 50 mm) spends only a few days in stream habitats before migrating to the lake during January through March (peaking in late February). The second group ("late fish") rear in tributary streams for several weeks before entering Lake Washington during April through late June (peak in mid-May). Juvenile Chinook salmon in the lake are consistently larger than those measured at the downstream migrant traps during the same week (Figure 2). The proportion of early and late fish varies annually both within and between tributaries (Seiler et al. 2004). Most juvenile Chinook salmon leave Lake Washington and enter Puget Sound in June and July (DeVries et al. 2004).
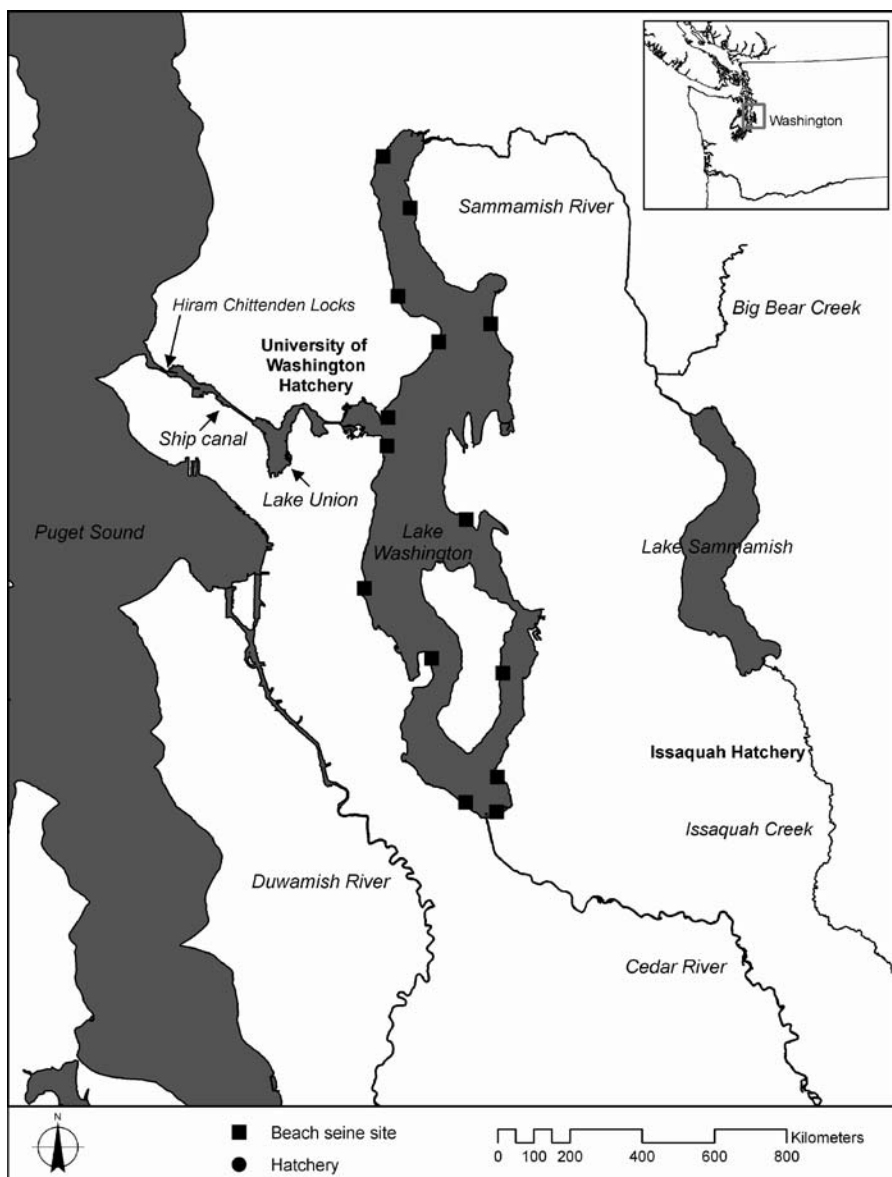
FIGURE 1.—Map showing the Lake Washington Ship Canal, and Howard Chittenden Locks, hatcheries, and beach seining sites throughout Lake Washington, where juvenile Chinook salmon were collected for an evaluation of diet and bioenergetics.

There are two salmon hatcheries in the basin—at Issaquah Creek and the University of Washington (UW); both release most of their Chinook salmon as fingerlings (>80 mm FL). Issaquah Creek Hatchery fish rear in Lake Washington, while the UW Hatchery fish appear to leave the system through the ship canal shortly after release. In 1999, the Issaquah Creek Hatchery released 2.2 million juvenile Chinook salmon between 4 and 13 May; in 2000, they released 1.5 million fish between 10 and 26 May.

Methods

Diet composition.

Stomach contents were retained from juvenile Chinook salmon collected throughout Lake Washington during February through June 1999 and 2000. Sampling sites were arrayed throughout the lake and included the range of littoral habitats available to the fish. Fish were collected at each site with a 37-m beach seine set to capture fish within approximately 33 m of the shoreline.
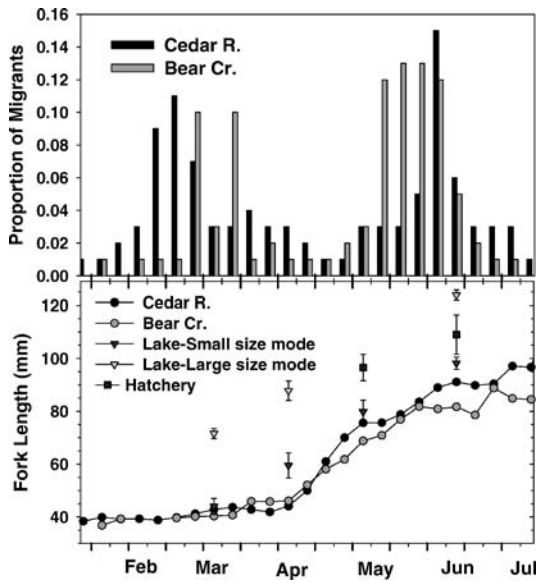
FIGURE 2.—Immigration timing of early and late juvenile Chinook salmon entering Lake Washington from the Cedar River and Bear Creek during 2000 (upper panel), and the mean fork length (FL ±SD) of wild and hatchery juveniles sampled monthly in the lake (triangles) or stream immigrants sampled weekly in migrant traps (circles and lines; lower panel).

Stomach contents of up to five individuals of each of three size-classes (<50, 51–100, and 101–150 mm FL) were obtained from each site once per month (Figure 1). In 2000, approximately 95% of juvenile Chinook salmon released from the Issaquah Creek Hatchery and approximately 100% from the UW Hatchery were released with adipose fins removed. In 2000, we distinguished fish that had an intact adipose fin (presumed naturally produced) and those without an adipose fin (marked hatchery-origin fish) before separating into size-classes. Hatchery fish were not marked in 1999.

After capture, juvenile Chinook salmon were anesthetized with MS-222 (tricaine methanesulfonate), weighed to the nearest 0.01 g and measured to the nearest 1 mm FL. Stomach contents were removed using a gastric lavage method similar to that described by Haley (1998). A hand-operated, pressurized, garden-type pump sprayer fitted with a 3-mm-diameter copper pipe with rounded edges was inserted into the fish's esophagus. Water pressure from the pump flushed stomach contents onto a 250-μm mesh sieve. Contents were preserved in a 70% solution of ethanol for later examination. Organisms were identified with a dissecting microscope. Small benthic and planktonic crustaceans and a few other taxa were identified to

genus or species. However, for most other major prey items, such as insects, identification was only practical to the order or family level. Each prey category was enumerated and weighed (blotted wet weight to the nearest 0.0001 g).

Differences in diet composition were examined with a one-way analysis of similarity (ANOSIM) using Primer version 5 (Clarke 1993; Marchant et al. 2000) and expressed as the R-statistic. The R-statistic measures magnitude of effect; R-values closer to 1.0 occur when across-group similarities are lower than those within groups. An R-value of 1.0 implies complete separation of groups (see Huff et al. 2005).

Bioenergetics.

We used the Wisconsin bioenergetics model (Hanson et al. 1997) to evaluate consumption and growth performance by juvenile Chinook salmon in Lake Washington. This model uses an energy balance equation that estimates the consumption of prey biomass needed to achieve a growth rate over a specific time interval while satisfying metabolic demands and waste losses:

$$\text{Consumption} = \text{metabolism} + \text{waste} + \text{growth.}$$

The model accounts for body mass, temperature, diet composition, and energy densities (J/g) of both consumer and prey on a daily time step when computing rates of maximum consumption, metabolism, and waste. It estimates the amount of consumption required to satisfy the growth observed by fish of a given initial body mass over a prescribed time interval, given the diet composition and temperatures experienced. Model estimates of consumption by juvenile salmon have been within 10% of independent field- and laboratory-generated estimates (Beauchamp et al. 1989; Brodeur et al. 1992; Ruggerone and Rogers 1992). The value $p(C_{max})$ fitted by the model represents the proportion of the maximum possible ration consumed by a fish of a given size and thermal experience. Values of $p(C_{max})$ can range from 0.0 to 1.0; values near 1.0 suggest that fish are feeding close to their maximum daily ration. Growth efficiency (GE), the body mass gained divided by the mass of food consumed, provides a complementary measure of growth performance that evaluates how well a fish grows in response to the integrated effects of food quality (energy density), food availability, and temperature-dependent effects on metabolism. For instance, eating an equal mass of prey with higher energy density will result in higher growth and improved GE relative to eating prey of lower energy density.

Model simulations were conducted using the Wisconsin bioenergetics model version 3.0 software

TABLE 1.—Thermal experience used in bioenergetics model simulations of juvenile Chinook salmon occupying the littoral region of Lake Washington during winter–spring 2000.

Day	Temperature °C
1	8.6
38	7.5
67	8.0
69	7.5
73	7.3
74	6.8
75	7.9
95	9.1
97	8.5
101	10.0
104	12.9
122	12.2
123	11.9
124	10.9
129	12.5
159	14.4
160	13.9
165	14.3
167	14.8
168	14.5
201	18.0
231	21.7
365	8.5

(Hanson et al. 1997). Model parameters provided by the software came from the general model for Chinook salmon (Stewart and Ibarra 1991). The input variables for these simulations were from field data on thermal experience, diet, prey, prey energy densities, and fish size.

Thermal experience.

Thermal experience of the fish was based on temperature data (1-m depth) taken concurrently with each beach seine sample during fish collections in littoral areas (Table 1). Average monthly temperatures used in simulations ranged from 7.8°C in February to 14.2°C in June. We believe these values provide a reasonable representation of thermal experience since the fish were closely associated with littoral areas until temperatures exceeded about 17°C in late spring and early summer, at which time they moved offshore (Tabor et al. 2004).

Diet composition.

Diet composition was derived from monthly diet samples (Table 2). Energy density values of the major prey items were taken from the literature and other sources and include *Daphnia* (Luecke and Brandt 1993), chironomids, and other insects (Beauchamp et al. 2004; Gray 2005).

Simulations and fish size.

Separate growth cohorts of juvenile Chinook salmon, representing primary life history groups using littoral habitats of Lake Washington during winter and spring 2000, were simulated (Figure 2). Life history groups were identified by tracking the size modes from migrant trap samples during peak migration through subsequent sampling dates in the lake. The majority of early juveniles migrated from the Cedar River, whereas later, larger migrants entered from Bear Creek and the Cedar River in similar numbers (Seiler et al. 2003).

The model simulations computed consumption rates on major prey categories, proportion of maximum daily ration ($p[C_{max}]$), and GE during monthly growth increments for wild and hatchery fish during lake residence. Growth scenarios were simulated for the late migrant pulses from both the Cedar River and Bear Creek based on the size of juveniles captured in downstream traps in May and in the lake in May and June (Table 3). Feeding and growth were also simulated for hatchery fish that entered the lake after release from local hatcheries on 10 May 2000. The simulation started with a weight in May of 10.1 g (average weight of identifiable size modes of hatchery

TABLE 2.—Diet inputs for Lake Washington Chinook salmon bioenergetics simulations. Prey energy densities are in parentheses.

Day	Chironomid larvae (2,478 J/g)	Chironomid pupae (3,400 J/g)	Chironomid adults (4,500 J/g)	Zooplankton (3,976 J/g)	Terrestrial invertebrates (4,500 J/g)	Other prey (4,500 J/g)
			Wild			
55	0.022	0.889	0.035		0.015	0.039
70	0.033	0.701	0.078	0.020		0.168
100	0.010	0.628	0.081	0.002	0.042	0.235
130	0.017	0.531	0.089	0.003	0.031	0.330
170		0.173	0.014	0.488	0.026	0.298
			Hatchery			
55						
70						
100						
130	0.017	0.531	0.089	0.003	0.031	0.330
170	0.001	0.272	0.010	0.331	0.042	0.344

TABLE 3.—Simulation cohorts of juvenile Chinook salmon during peak migration from the Cedar River Washington (25 February 2000) and subsequent monthly growth increments in Lake Washington through 9 June 2000. The initial and final days and body masses (W_i and W_f, respectively) for each growth increment are indicated, as is the resulting fitted P-value, estimated consumption (C; g), and growth efficiency (GE) over the growth interval.

Simulation cohort	Day	Wt_i	Wt_f	P-value	C	GE (%)
Smaller-sized early migrant pulse						
Cedar River 25 Feb–Lake 11 Mar	55–70	0.6	0.9	0.67	1.7	17
Lake 11 Mar–Lake 10 May	70–130	0.9	5.6	0.83	25.4	19
Lake 10 May–Lake 9 Jun	130–160	5.6	11.5	0.80	33.0	18
Larger early lake-rearing						
Lake 11 Mar–Lake 10 Apr	70–100	4.0	8.1	0.95	22.6	18
Lake 10 Apr–Lake 9 Jun	100–160	8.1	24.0	0.78	95.8	17
Late migrant pulse						
Cedar River 10 May–Lake 9 Jun	130–160	4.8	8.6	0.66	23.1	16
Bear Creek 10 May–Lake 9 Jun	130–160	3.6	6.1	0.58	16.1	16
Issaquah Hatchery release						
Lake 10 May–Lake 9 Jun	130–160	10.1	15.3	0.60	34.0	15

Chinook salmon caught in May) and ended at 15.3 g in June. All simulations ended on 9 June, corresponding to the mid-June period when fish leave the littoral and limnetic zones and migrate from the lake (DeVries et al. 2004).

The discrete immigration pulses and narrow size range of fry measured at the migrant traps on the Cedar River and Bear Creek enabled us to track identifiable size modes in the monthly sampling periods from February to June. These size modes defined the initial and final weights used by the bioenergetics model to fit consumption rates that satisfied the observed growth increments (). We assumed that emigration from the lake was not significant until June–July based on the observations of migrants through the navigation locks into Puget Sound by DeVries et al. (2004). The majority of the population was represented by the small early migrant size mode in the lake (Figure 2; Seiler et al. 2003). Because identification of the size mode for the small early migrants was somewhat ambiguous during April, we fitted consumption in the model to growth between the easily identifiable size modes on 11 March and 10 May (). For example, the first simulation was run for the peak early immigration of wild Chinook salmon fry that entered the lake on an average date of 25 February 2000 (simulation day 55) at a FL equal to 40 mm and a body mass of 0.6 g; this pulse was tracked to a modal size of 44 mm FL (SD = 3) and 0.9 g in the next lake sample on 11 March, then to 80 mm FL (SD = 4) and 5.6 g (SD =1.3) on 10 May, and 98 mm FL (SD = 2) and 11.5 g (SD = 1.5) on 9 June 2000 (Table 3).

Growth rates were converted to lineal rates (mm/d) for comparison with juvenile Chinook salmon from other populations. Simulated growth rates from the model were converted from weight (WT) to FL by rearranging the length–weight regression for the lake population ($r^2 = 0.978$; $N = 500$; $P < 0.00001$):

$$WT = 0.000006 \cdot FL^{3.16073}$$

to

$$FL = (WT/0.000006)^{0.31638}.$$

Growth (mm/d) was estimated by computing the difference between the initial and final FL divided by number of days within the growth interval.

Results

Immigration Timing, Size, and Growth of Juvenile Chinook Salmon

Monthly mean FL and weights of the fish were similar in 1999 and 2000 (Table 4). Based on migrant trap results that started in early January, juvenile Chinook salmon immigrated into the lake in two major pulses, and peaks occurred in late February and from mid-May to early June (Figure 2). After the early peak in fry, two size modes of wild juvenile Chinook salmon occurred in lake samples in March (Figure 2). The smaller size mode clearly corresponded to the peak migration of early migrants in late February and was tracked monthly through 9 June 2000 (Figure 2). In contrast, the source of the larger size mode could not be reconciled with the size or timing of fish in the migrant traps because they were too large to have originated from the initial peak migration in late February. Exploratory bioenergetics modeling indicated that under ambient thermal conditions and maximum daily rations, even migrants from early January could not have achieved the sizes observed in March.

Wild juveniles from both size modes in the lake in February were consistently larger than those migrating out of the streams later in the season (Figure 2). In contrast, sizes of juveniles sampled in the lake from the May–June immigration pulse were similar to those of

TABLE 4.—Mean (M), sample size (N), SD, test statistic (t), df, and P-value for t-tests comparing the size of juvenile Chinook salmon in Lake Washington in 1999 and 2000 ($\alpha = 0.05$).

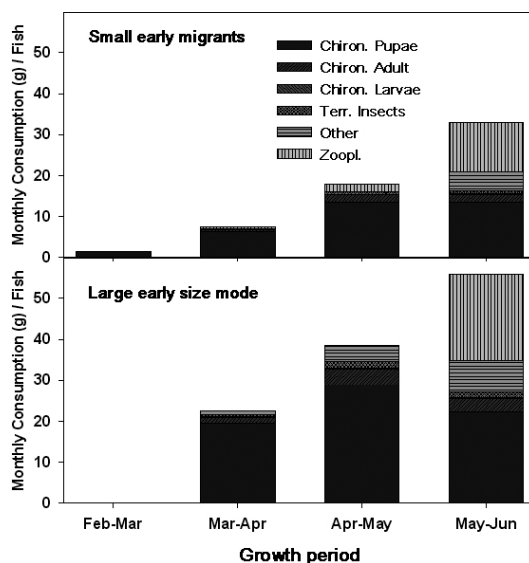| Month	M	N	SD	t	df	P-value
Fork length (mm)						
Mar 1999	54	33	14.5			
Mar 2000	56	38	15.2	0.08	69	>0.5
Apr 1999	57	40	12.2			
Apr 2000	64	32	15.8	0.59	70	>0.5
May 1999	96	56	22.9			
May 2000	76	38	12.8	1.06	92	>0.2
Jun 1999	102	98	10.3			
Jun 2000	109	114	16.3	0.049	210	>0.5
Total 1999	83	241	26.8			
Total 2000	88	222	27.1	0.17	461	>0.5
Weight (g)						
Mar 1999	1.6	33	1.99			
Mar 2000	2.3	38	1.75	0.38	69	>0.5
Apr 1999	2.4	40	1.46			
Apr 2000	4.0	32	2.66	0.81	70	>0.5
May 1999	9.3	56	5.50			
May 2000	5.1	38	12.8	0.50	92	>0.5
Jun 1999	11.8	98	3.76			
Jun 2000	15.4	114	5.22	0.79	210	>0.5
Total 1999	7.5	241	5.80			
Total 2000	9.7	222	7.17	0.35	461	>0.5

FIGURE 3.—Bioenergetics model estimates of monthly consumption rates and biomass contributions of major prey taxa eaten by two early rearing size modes of juvenile Chinook salmon in Lake Washington during February–June 2000. The "other" prey category includes larval fish, epibenthic crustaceans, copepods, and *Neomysis mercedis*. February data are from 1999; March–June data are from 2000.

the migrants sampled concurrently in the downstream traps. The sizes of hatchery fish were more variable than those of the wild cohorts, but one strong unimodal size-group was recognizable in both May and June, as it had mean sizes significantly larger than all but the largest of the wild cohorts (Figure 2).

Diet Composition

The diet composition of 463 juvenile Chinook salmon sampled from the Lake was dominated by chironomids until June, when *Daphnia* spp. became the primary prey. Numerical composition and frequency of occurrence generally tracked the biomass contribution by all prey types. However, terrestrial prey occurred more frequently in the diets (48–51%) than was represented in the total prey biomass (2–5%). Other prey included larval fish, epibenthic crustaceans, copepods, and the mysid *Neomysis mercedis*. Diet compositions were similar among fish of different sizes (FL) within April (ANOSIM: global $R = 0.30$, $P = 0.08$), May (global $R = 0.23$, $P = 0.12$), and June (global $R = 0.10$, $P = 0.04$) and between the 1999 and 2000 seasons (global $R = 0.22$, $P = 0.06$). Considerable diet overlap was evident between hatchery and wild juvenile Chinook salmon in June 2000 (global $R = 0.11$, $P < 0.05$).

Bioenergetics

The model simulations indicated that all growth cohorts of juvenile wild and hatchery Chinook salmon fed at relatively high consumption rates ($p[C_{max}] = 58–90\%$ of the maximum daily ration) experienced high GEs (15–19%) in simulations for February–June (Table 3). When all cohorts occurred together in the lake in May–June, the later pulse of wild migrants and hatchery fish exhibited lower consumption rates ($p[C_{max}] = 58–66\%$) and GEs (15–16%) than either the small or large size modes that entered the lake in February or earlier ($p[C_{max}] = 79–95\%$; GE = 17–19%) (Table 3).

From 25 February to 9 June 2000, modeled consumption rates increased monthly as both temperatures and body sizes of the Chinook salmon increased (Figure 3). Chironomids (primarily pupae) contributed 70% of the prey biomass consumed by both the small and large early size modes rearing in the lake, whereas zooplankton contributed only 17% of the biomass and became important only during the final monthly growth interval (May–June) in the lake (Figure 3).

The May–June growth interval was the only period when Issaquah Hatchery fish and the second pulse of migrants from Bear Creek and the Cedar River commingled with the earlier migrants. The two early migrant groups exhibited high feeding rates ($p[C_{max}] = 78–80\%$), whereas the later wild and hatchery arrivals all exhibited moderate feeding rates ($p[C_{max}] = 58–$
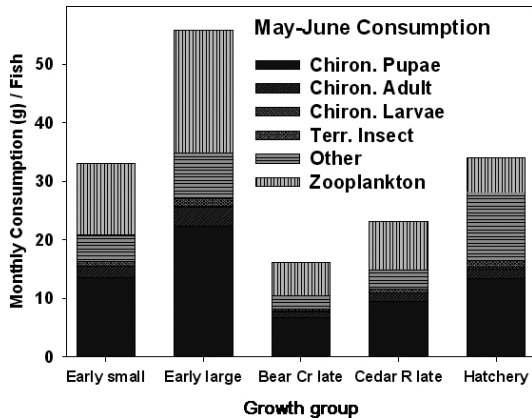
FIGURE 4.—Bioenergetics model estimates of monthly consumption rates and biomass contributions of major prey taxa eaten by all life history types of juvenile Chinook salmon co-occurring in Lake Washington from 10 May to 9 June 2000.

66%; Table 3; Figure 4). The larger body size of hatchery fish, combined with the moderate $p(C_{max})$, resulted in a relatively high biomass of prey consumed during the May–June growth interval.

Growth rates were low for the small size mode in February–March (0.36 mm/d) but increased to 0.50–0.67 mm/d for both size modes of early migrants March–June. The later wild migrants and hatchery fish grew at a slower rate in May–June (0.42–0.51 mm/d) than the early migrants.

Discussion

Lake residence is a rare life history strategy for ocean-type Chinook salmon (e.g., Burger et al. 1985), but our results suggest that the juvenile Chinook salmon can feed and grow well in this habitat. The results of our model simulations (e.g., GEs and $p[C_{max}]$) suggested that naturally produced juvenile Chinook salmon were finding ample food in littoral habitats of Lake Washington. For example, our values of $p(C_{max})$ were usually greater than 60% and indicate that juveniles were feeding close to their maximum ration. In fact, our bioenergetics simulations indicated that the wild Chinook salmon fry spending the longest time in the lake (i.e., earliest entrants) exhibited the highest weight gains, highest daily consumption rates, and the best GEs of all modeled cohorts. While the later lake entrants showed lower growth than early entrants, the estimated lineal growth rates from this study generally compared favorably with growth rates of Chinook salmon rearing in other habitat types (Table 5). For example, lineal growth in Lake Washington was similar to or greater than growth reported in river

channel and estuarine habitats in the Sacramento–San Joaquin River basin, and similar to estuarine and nearshore marine growth in Puget Sound.

The growth exhibited by naturally produced juvenile Chinook salmon in littoral areas was largely a result of two prey items: chironomids (February to May) and *Daphnia* (May and June). The shift in diet of juvenile Chinook salmon from insects to *Daphnia* probably resulted from a combination of habitat shifts by the fish, environmental changes in the lake, and seasonal changes in production of prey. The diet shift occurred at the same time as *Daphnia* production in Lake Washington dramatically increases each year when they become the dominant zooplankter during spring through early fall (Edmondson and Litt 1982). At the same time as *Daphnia* production increases, the density of chironomid larvae in the littoral benthos of Lake Washington does not decrease (Koehler 2002), suggesting that the diet shift was not due to a decline in the insect production. When the fish switched to feeding on *Daphnia*, juvenile Chinook salmon were becoming more abundant in limnetic habitats (R. Tabor, U.S. Fish and Wildlife Service, and K.L.F., unpublished data). The shift in fish distribution and diet also coincided with increasing fish body size and increasing littoral zone water temperatures and was similar to habitat shifts reported in Snake River reservoirs (Curet 1993).

Even after large numbers of hatchery-produced juvenile Chinook salmon entered the lake, the high modeled GEs and $p(C_{max})$ of both types of fish when they co-occurred suggested that they were not competing for food under current conditions. We hypothesize that the high GEs and growth rates of hatchery- and naturally produced Chinook salmon is a function of both types of fish preying primarily upon the abundant zooplankton *Daphnia* spp. When both hatchery- and naturally produced juvenile Chinook salmon were present in the lake, *Daphnia* dominated the diets of both groups. After the *Daphnia* population increased in May, consumption by the entire planktivorous fish community (including juvenile Chinook salmon) apparently represented only a small fraction of the biomass or production of *Daphnia* in the lake (e.g., Beauchamp 1996).

While current hatchery practices do not appear to adversely affect growth of naturally produced Chinook salmon, changes in hatchery practices (e.g., increase in numbers of hatchery fish) could potentially increase competition between hatchery and wild fish. Of particular concern is a change in the release timing of the hatchery fish so they arrive in the lake before the *Daphnia* bloom, when chironomids are the primary prey. It is unclear whether there would be sufficient

TABLE 5.—Modeled growth rates (mm/d) for Chinook salmon fry rearing in Lake Washington, and estimated growth exhibited by Chinook salmon in non-lake rearing habitats.

Fry type	Months	Location	Habitat	Growth (mm/d)	Source
Wild	Feb–Mar	Lake Washington	Lake (littoral zone)	0.36	This study
Wild early	Mar–Jun	Lake Washington	Lake (littoral zone)	0.50–0.67	This study
Wild late	May–Jun	Lake Washington	Lake (littoral zone)	0.42–0.51	This study
Wild	Feb–Jun	Lake Washington	Lake (littoral zone)	0.71	This study
Hatchery	May–Jun	Lake Washington	Lake (littoral zone)	0.45	This study
Hatchery and wild	May–Jul	Puget Sound	Estuary and Nearshore marine	0.29–1.02 0.62	Duffy 2003
Wild		Sacramento–San Joaquin River, California	Estuary	0.53	Kjelson et al. 1982
Wild		Nanaimo River	Estuary	1.32	Healey 1980
Wild	May–Sep	Campbell River, BC	Estuary	0.46–0.55	Levings et al. 1986
Hatchery	Mar–May	Puyallup River	Estuary	0.37	Shreffler et al. 1990
Hatchery	Jan–Apr	Yolo Bypass	Agricultural floodplain	0.55–0.80	Sommer et al. 2001
Wild		Sacramento–San Joaquin River	River channel	0.33	Kjelson et al. 1982
Hatchery	Jan–Apr	Sacramento River	River channel	0.43–0.52	Sommer et al. 2001

chironomids to support current populations of both hatchery- and natural-origin Chinook salmon.

The modeling approach we employed tracked discrete cohorts of fish, each cohort representing a different arrival time into the lake (e.g., early or late) or fish type (hatchery or wild). Each cohort thus represented an average condition for a particular cohort. One concern with such an approach is that increasing variability in body weight as length increases might bias results. We believe our cohort means are reasonable because we had adequate sample sizes, could find no obvious biases in sample collection, and we constructed our cohorts based upon specific emigration data into Lake Washington. Using an individual-based modeling approach is one alternative to our cohort approach; this would require tracking individual fish to construct individual growth trajectories. Clearly, several factors could affect mean sizes of cohorts, including whether or not the population was closed and size-selective mortality. While significant emigration from the lake does not occur until June-July (DeVries et al. 2004), there may have been some immigration from other populations for which we could not account. We believe the likelihood of immigration into our cohorts was low based upon the low numbers of Chinook salmon spawning in the smaller tributaries to the lake (K.L.F., personal observation). If size-selective mortality occurred, then we could have overestimated the true growth rate. Although we could not detect removal of smaller individuals in the changing size-frequency distributions, this observation does not represent a rigorous examination of this possibility. This would require an analysis of individual performance, such as scale or otolith samples (Moss et al. 2005), which was beyond the scope of this study.

It is not clear from our study if the heavily developed shoreline in Lake Washington has impacted juvenile Chinook salmon prey in the littoral zone. Toft (2001) estimated that nearly all of the shoreline of Lake Washington had some type of development (armoring, pier, or dock) and classified only 5% as "natural." In Lake Washington, densities of shallow-water, benthic chironomid larvae are lower in areas that are heavily urbanized or commercially developed than in natural areas (Koehler 2002). Other studies in lakes also suggest that shoreline development alters invertebrate communities (White 1975; Northcote and Northcote 1996; Schmude et al. 1998). Shoreline modifications such as revetments, docks, and piers can depress chironomid densities (Armitage et al. 1995), and retained shorelines are associated with lower invertebrate diversity and abundances than are found along natural shorelines (Northcote and Northcote 1996).

The results of our study suggested that one effect of shoreline development in Lake Washington may have been to reduce the availability of terrestrial-origin prey. Although prominent in diets in other lacustrine settings (Clemens 1934; Rondorf et al. 1990; Busby and Barnhart 1995), terrestrial prey did not contribute materially to either the numerical or gravimetric composition of juvenile Chinook salmon diets in this study (5% and 2% of total consumed biomass in 1999 and 2000). Terrestrial prey did, however, occur frequently in Chinook salmon stomachs. The availability of terrestrial prey appears to be low in the lake based on the results of neuston samples collected during the study period; these samples contained very few terrestrial organisms (0.0–0.9 organisms/m^2; Koehler 2002). Historically, Lake Washington was surrounded with old-growth coniferous forest, emergent marsh, shrub–scrub, and deciduous riparian

habitats (Chrzastowski 1983) that would be expected to provide various types of invertebrate prey (e.g., aphids, wasps, spiders) for fish (Kawaguchi and Nakano 2001; Allan et al. 2003). The low numbers of terrestrial organisms in neuston and fish diet samples could therefore result from the replacement of natural riparian vegetation with riprap, bulkheads, and other impervious surfaces.

Although our results suggest that juvenile Chinook salmon are currently feeding and growing well in lacustrine habitats, a variety of changes could adversely affect growth in future years. Major human-induced limnological changes (e.g., water quality and introduced species) have been well chronicled in Lake Washington (Edmondson 1991), and the lake may be vulnerable to future, large-scale perturbations caused by continuing human activities (e.g., climate change, water quality). Large-scale changes that alter characteristics of the prey community or predator–prey dynamics such as a decline in *Daphnia* densities due to temporal mismatches with phytoplankton production (Winder and Schindler 2004), altered timing of releases of hatchery fish, increased abundance of hatchery fish, or decreased consumption rates due to high turbidities could increase the potential for food limitations. Given the reliance of Lake Washington juvenile Chinook salmon on only two main prey types (chironomids and *Daphnia*), it may be prudent for resource managers to help diversify the prey available to the fish. This could buffer Chinook salmon from the effects of large-scale ecological changes in the lake ecosystem. One way to accomplish this would be by preserving existing vegetated riparian areas and creating new vegetated areas around the lake. These riparian areas could increase terrestrial invertebrate production in Lake Washington and thereby diversify the amount and type of food available for the juvenile Chinook salmon. In addition, terrestrial insects have relatively high caloric values (Gray 2005).

Despite the heavily altered nature of Lake Washington and the relatively short time span Chinook salmon have used this system, feeding and growth performance of juvenile Chinook salmon in littoral habitats of Lake Washington were comparable to those for Chinook salmon rearing in estuarine and riverine environments (e.g., Healey 1982; Simenstad et al. 1982; Rondorf et al. 1990; Miller and Simenstad 1997; Duffy 2003) (Table 5). This suggests that increasing the amount food available to the juvenile Chinook salmon in Lake Washington will not materially contribute to efforts to improve the status of this population. Efforts to rebuild Chinook salmon populations in this basin should therefore focus on the influence of other lake-related factors, such as

predation and disease, and other life stages (e.g., spawning adults). For example, Lake Washington has an extensive piscivore community, including cutthroat trout *O. clarkii* (Nowak et al. 2004), northern pikeminnow *Ptychocheilus oregonensis* (Brocksmith 1999), largemouth bass *Micropterus salmoides*, and smallmouth bass *M. dolomieu* (Fayram and Sibley 2000). Studies of other anadromous populations in this system suggest that predation is probably a major limiting factor for these populations (Nowak et al. 2004). Whether or not juvenile Chinook salmon in the lake are similarly affected by predation requires further study.

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